Chapter (non-refereed)

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BRANCHING, CROWN STRUCTURE AND THE CONTROL OF TIMBER PRODUCTION

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I. INTRODUCTION

The rate of timber production by a forest is dependent upon the size and functioning of tree crowns. Spacing and thinning, the most widely practised silvicultural operations, influence both total stand volume increment and its distribution between differently sized trees, because they influence tree crown structure and function (Assmann 1970). The empirical relationships on which these silvicultural operations are based have their origins in research initiated over 100 years ago, yet attempts to increase timber yield by selecting and breeding trees with particular crown structures are still in their infancy.

One theory, discussed by both Dickmann and by Kärki and Tigerstedt in

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this volume, is that sparsely branched tree genotypes can produce greater amounts of stemwood than heavily branched genotypes. This hypothesis seems to be counter-intuitive, which highlights our need to understand (a) the interaction between branch growth, crown development and the control of timber production, and (b) intraspecific differences in these interactions, and how they may be exploited.

Three factors complicate the study of these problems. First, there are differences between tree species in crown form, and in the anatomical and morphological processes by which crowns are produced. Second, tree branches perform functions other than the production of stemwood. Natural selection operates through breeding success, and branching structures may have evolved, at least in part, to ensure the efficient display of reproductive organs, or to shade neighbouring plants. Third, branch production and growth are influenced by a wide range of environmental factors, and it can be difficult to isolate their separate influences on stemwood production.

The operation of a complex of factors in controlling branch growth and crown development, and the problems these pose to scientific study, are apparent in the descriptions and classifications which have been made of branching patterns and crown forms. Most frequently, both qualitative and quantitative models have been developed for single aspects of branch growth and function. These models are reviewed here, and are used to interpret empirical evidence on the relationship between crown form and stemwood production in single trees, and to develop a discussion about factors controlling timber production in stands.

II. CLASSIFICATIONS AND DESCRIPTIONS OF BRANCHING AND CROWN FORM

Tree species have been classified into a few crown or morphological types, which suggests that, during evolution, certain morphological and physiological requirements have been met repeatedly in similar ways. Hallé *et al.* (1978) classified tropical trees into 23 architectural models. They defined architecture as the 'morphological expression of the genetic blueprint', and stressed that this included developmental sequences. Their dichotomous key is based on characters of the primary meristem, such as its lifespan – which determines whether growth is monopodial or sympodial, its pattern of differentiation to sexual or vegetative growth, and its orientation to give plagiotropic or orthotropic shoots.

Brunig (1976) produced a classification of 12 prototype crown architectures based on ecophysiological principles – mainly the aerodynamic properties of leaves and tree shape, which influence the exposure of mature leaves to radiation and wind. The balance between light interception, and the requirement to invest material in branchwood, was also considered. Brunig's classification was based on visual observations of broad differences among tree crowns along vegetational gradients, in both tropical and temperate forests. For example, he described forests growing along a catena, ranging from tall, large-leaved broad crowns on a mesic latosol to short, small-leaved forms on a xeric podsol.

Brunig (1976) considered his classification to be an initial approach. For the precise use of trees as crop plants we need to be able to describe crown form functionally – in relation to its branching structure (how the tree grows) and its efficiency in timber production (how the crown works).

A. Branching morphology

A wide variety of tree crown forms can arise from variation in a few branching rules. This fact has important implications when framing hypotheses about the mechanisms that control branching. Tree crowns are comprised of three basic types of shoot: the main stem, the branches or 'long shoots', which frequently have indeterminate growth, and 'short shoots', which may carry a large proportion of the foliage, but which have little influence on crown form.

Four categories of main stem can develop from terminal and axillary meristems, as illustrated in Figure 1. (a) A single apical meristem may remain active throughout the life of the tree (Fig. 1A). (b) A bifurcating apical meristem may give dichotomous branching with equal branch development, or one branch may develop reproductive organs giving sympodial growth (Fig. 1B). (c) The apical meristem may generate a number of meristems of

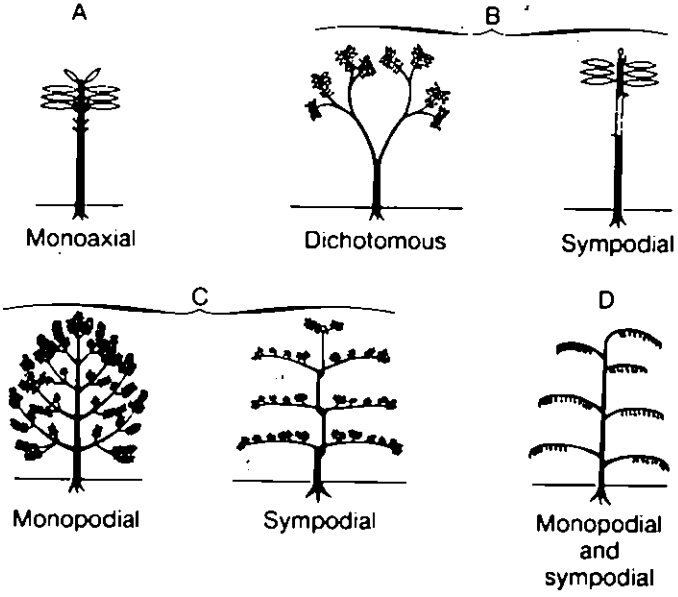

FIGURE 1. Four categories of main stem branching and development in trees, and their influence on crown shapes.

A. Only the main stem extends.
B. Left: bifurcation with equal vegetative axes; right: bifurcation with vegetative and reproductive axes.
C. Main stems and branches have unequal growth potentials.
D. Main stems and branches have equal but mixed growth potentials.

unequal growth potential, producing crowns with orthotropic main stems. These can be monopodiums, or sympodiums – where the main stem develops from a lateral shoot either with (proleptically) or without (sylleptically) a period of correlative inhibition (see below) from the apical bud (Fig. 1C). (d) Main stem branches may be produced by multiplication of the apical meristem, giving shoots which, at different times, may become branches or main stems (Fig. 1D). Both monopodial and sympodial types occur. Branch-like (plagiotropic) main stem tips can later become erect by producing reaction wood and, in sympodial types, erect main stems may become plagiotropic.

Lateral shoots originate from meristems in the axils of leaves, or, in a few genera such as *Picea*, from meristems apparently differentiated from internode cortical tissues. *Apical dominance* is the suppression, by the terminal apex, of buds on the current year's shoot, and can occur both before or after a period of branch growth (see Phillips 1975). *Apical control* is the partial or complete inhibition of lateral shoot elongation by the influence of one or more distal apices (Fig. 2) (Brown *et al.* 1967). Broadleaved temperate trees with narrow excurrent crowns, such as *Populus*, have leading shoots with weak apical dominance (over the current year's buds) but strong apical control (over the previous year's shoots), while those with spreading, decurrent crowns have

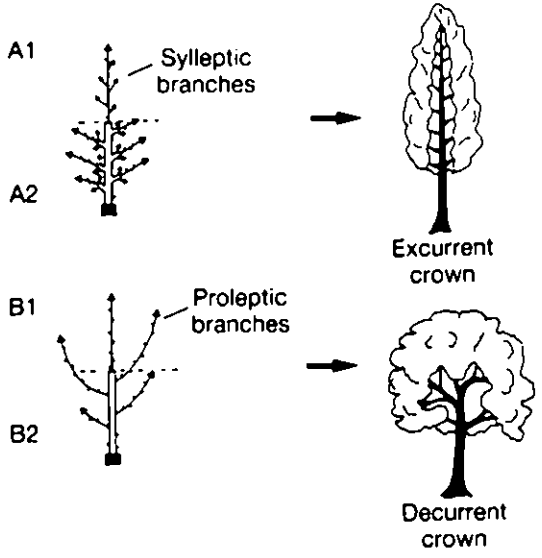

FIGURE 2. Schematic relationship between apical dominance, apical control, and the development of excurrent and decurrent crowns on broadleaved trees.

A1. Weak apical dominance of buds on the current year's shoot.

A2. Strong apical control, restricting the growth of shoots produced in previous years.

B1. Strong apical dominance, preventing the growth of buds on the current year's shoot.

B2. Weak apical control, allowing the active growth of buds produced in previous years.

strong apical dominance but weak apical control (Fig. 2). Shoots which are strongly suppressed by apical control, and produce a rosette of leaves with little internode elongation, are called 'short shoots', as are the needle fascicles of pines.

B. Generation of branching patterns

The shoot apices control branching, by influencing the number of lateral buds produced, the distance from the apex at which the buds develop (apical dominance), and the rate of growth of the lateral shoots relative to the main stem (apical control). Whilst the physiological control through hormonal, nutritional and other metabolic processes is still debated (Trewavas 1981), mathematical descriptions of branch generation have indicated an apparent underlying simplicity, which may be important in understanding both genetic and environmental influences.

Rozenberg and Lindenmayer (1973) used a simple recurrence formula to describe the development of a compound leaf as a branched structure, produced initially from a single apical cell. Suppose the cells of a leaf margin exist in ten states: $b, c, d, e, f, g, h, i, j, k$, with a as the single starting state, and ten transition rules govern the developmental sequence: $a \rightarrow bc$, $b \rightarrow kd$, $c \rightarrow ek$, $d \rightarrow gb$, $e \rightarrow cf$, $f \rightarrow ih$, $g \rightarrow hi$, $h \rightarrow de$, $i \rightarrow k$, and $k \rightarrow k$. These rules produce the following successive generations,

a

bc

kdek

kgbcfk

khikdekihk

kdek kgbcfk kdek

kgbcfj khikdekihk khbcfk

khikdekihk kdekkgbcfkkdek khikdekihk

Cells in stage k define non-growing portions of the leaf (notches) and occupy positions between developing adjacent leaflets. The last three generations of this developmental sequence are represented as stages of a developing leaf in Figures 3A, B and C. The centre part of each generation has a string of cells, which generates the entire string of two steps previously, while its left and right portions generate the entire string of three steps before. This can be written as a locally catenative formula for the nth generation, $n>5$,

$$\alpha_n = \alpha_{n-3}\ \alpha_{n-2}\ \alpha_{n-3} \qquad (1)$$

A locally catenative formula, which may have particular relevance to development morphology, has the form $\alpha_n = \alpha_{n-2}\,\alpha_{n-1}$. Starting from a single state,

this formula generates strings with lengths which are the consecutive numbers of the main fibonacci series (1, 2, 5, 8, 13, . .).

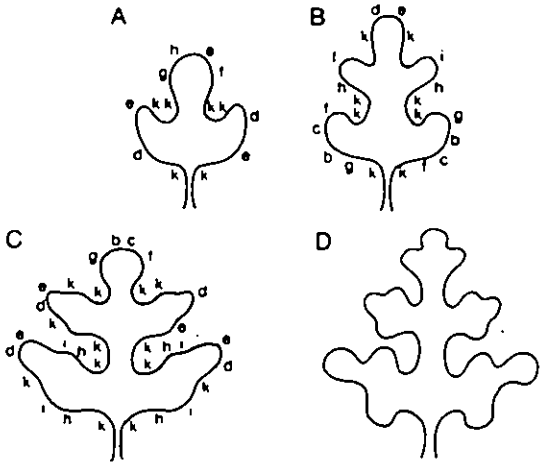

FIGURE 3. The development of a compound leaf, following a theoretical generation system with 10 basic states and 10 transformation rules between states. A, B and C illustrate stages of development to the final leaf form D (see text) (from Rozenburg & Lindenmayer 1976).

A change in just one transition rule can have a dramatic effect on the final pattern. For example, symmetry in the proposed development of the compound leaf is maintained by two of the transition rules, $g>hi$ and $f>ih$. A change in either, to produce just i, generates branches on only one side of the structure. Such dramatic changes in tree architecture do exist in nature (Hallé 1978). The shoots of cassava (*Manihot esculenta*) normally bifurcate dichotomously (as in Fig. 1B), but a sympodial form also occurs. The normal crown forms of *Pinus caribea* and *Hevea braziliensis* are as in the left of Figure 1C, but both species can produce single unbranched stems, termed 'foxtails' and 'lampbrushes', respectively. Hallé and Martin (1968) produced lampbrush trees of *Hevea* by removing most of the leaves when they were young. Hallé (1978) listed 21 architectural 'mutants' which involved substantial changes in branching pattern, although only some of them bred true. He also noted that considerable architectural polymorphism occurs in most taxonomic families, and in some genera, which, from an evolutionary standpoint, implies that within-species genetical varation in branching does occur.

Just as it is possible to represent bud production and orientation in a simple manner, so it is possible simply to describe the growth relationships between lateral branches and their parent shoot. Frijters and Lindenmayer (1976) advanced a simple formulation for 'paracladial' relationships, where branches repeat the inflorescence-like structure of the main axis. Only two variables were required: a delay period before the daughter branch began the repetition, b (akin to a measure of apical dominance), and a proportional growth rate, a (akin to a measure of apical control). Repeated application of linear formulae,

with constant values of a and b, produced the branching patterns observed in inflorescences, except that branching at the base was more prolific than actually observed (Fig. 4). This process can be improved upon if b, and particularly a, decline with increasing distances from the main stem apex. Frijters and Lindenmayer (1976) gave procedures for estimating the parameters of these recurrence formulae in real trees.

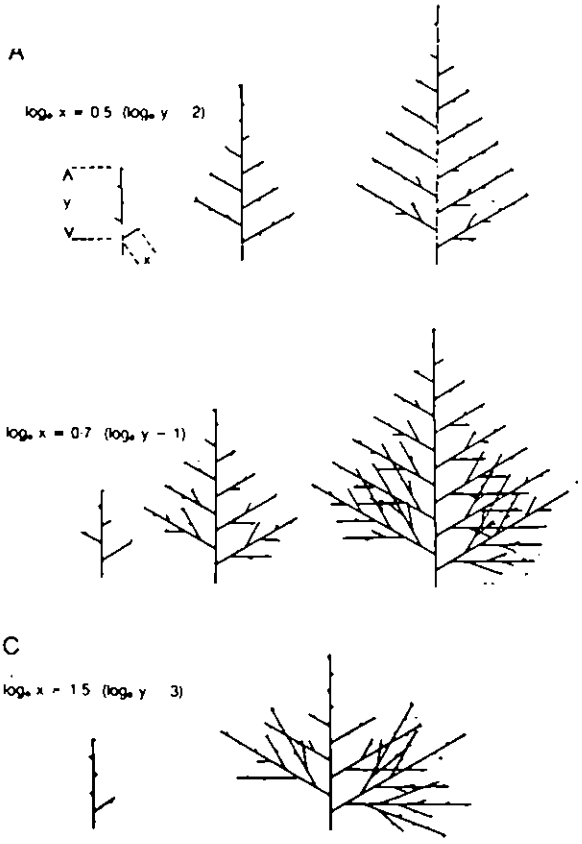

FIGURE 4. Generation of branched structures, with varying degrees of apical dominance, approximated by b (the delay in internode position before development starts) and apical control, approximated by a (the growth rate of the branch relative to that of the parent stem). In A, $a = 0{\cdot}5$ and $b = 2$; in B, $a = 0{\cdot}7$ and $b = 1$; in C, $a = 1{\cdot}5$ and $b = 3$ (from Frijters & Lindenmayer 1976).

C. Description of branching as a connected system

The bifurcation ratio, R_b, is a simple descriptive statistic of the branching structure as a connected system. It has been used to show how branching structures vary in a consistent way between broad taxonomic groups, at

different positions along an ecological gradient, in different environments, and in different parts of tree crowns.

To calculate R_b, branches are classified according to their order, where terminal sections have order 1 (Strahler 1957; Fig. 5). These join at nodes to give branch sections with order 2, and two order 2 branches join to form branches with order 3, and so on to the main stem. If two branches of different order meet, then the conjoined branch takes the same order as the higher of the two. Segments which form one contiguous branch of the same order are all considered part of the same branch (Fig. 5B). Note that, when applied to a living tree, the ordering system does not necessarily reflect the age of the shoots.

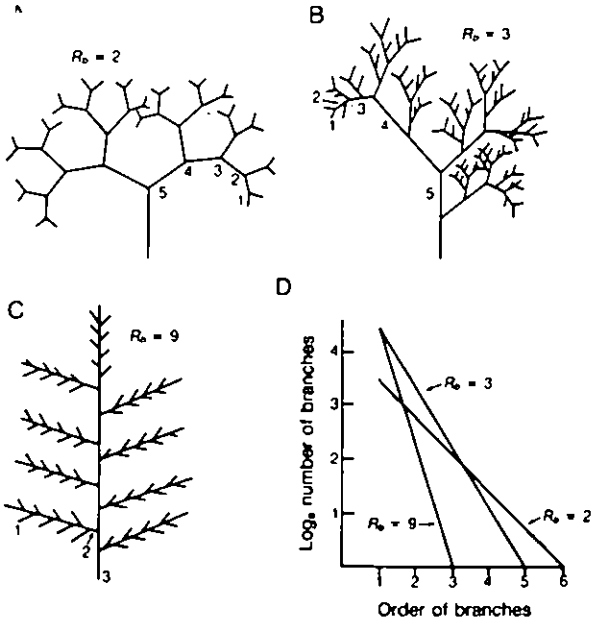

FIGURE 5. Examples of the bifurcation ratio, R_b, used to describe the branching structures of trees and other plants. In A, B and C, the numbers 1, 2, 3 . . . indicate the orders of branches.

The logarithm of the number of branches in each order, plotted against the order itself, typically gives a linear plot, and the antilog of the slope is the average bifurcation ratio, R_b, of the system; that is, there are R_b times as many branches in each order as in the next higher order, and the minimum value of R_b is 2·0 (Fig. 5). As will be discussed, R_b can vary within individual trees, and most workers have used the formula:

$$R_b = \frac{N - N_{max}}{N - N_2} \qquad (2)$$

where N is the total number of branches of all orders, N_{max} is the number of branches of the highest order (and will be 1 if the system is considered down

to the main stem) and N_1 is the number of branches of the first order, that is the endmost branches. Equation (2) averages the value of the bifurcation ratio over the whole system, giving slightly more weight to the more numerous lower order branches (Motomura 1947).

Oohata and Shidei (1971) measured the branching structures of contrasting tree species in Japan, 1·5–7·0 m tall and 2–10 cm in basal diameter, and found significant differences in R_b between species with different types of leaves, characteristic canopy sizes and foliage durations (Table I). Those with evergreen foliage, expecially those with leaves closely adpressed to the stem, and where the stem was an integral part of the foliage frond, had the highest values of R_b. Deciduous, broadleaved trees had the lowest R_b values. Typically, foliage areas are larger in evergreen, and in coniferous, forests than in deciduous and broadleaved forests. This characteristic seems to be related to their R_b values, as will be discussed below.

TABLE I. Branching ratios (R_b, see Fig. 5) of different tree life forms, measured in a forest near Kyoto, Japan. Mean R_b values are significantly different with $P<0·05$ (after Oohata & Shidei 1971)

	Numbers of		R_b		
	species	trees	Mean	Maximum	Minimum
Deciduous broadleaved	6	11	3·2	3·7	2·7
Evergreen broadleaved	9	16	4·4	5·9	3·1
Evergreen coniferous needle foliage		12	5·1	3·9	6·5
Evergreen coniferous leaves scale-like, adpressed to the stem	5	6	7·8	10·8	5·6

Branching patterns giving decurrent crowns, where apical dominance is high and apical control is low, tend to have low R_b values, whereas branching patterns giving excurrent crowns, where apical dominance is low and apical control is high, tend to have high R_b values (Fig. 2). The difference in R_b values between species broadly parallels their evolutionary advance in complexity of leaf type. For the primitive conifers, with adpressed leaves, Oohata and Shidei (1971) reported that the regression of $\log_e$ (branch number) on branch order could be extended to include the final 'leaf branch', although the numbers of these appeared to be slightly, but consistently, higher than expected in the five species examined. In contrast, for three deciduous species, leaf number was greater than would be predicted by extending the regression of $\log_e$ (branch number) on branch order to zero. However, Barker *et al.* (1973) reported that the number of winter buds on two deciduous species could be predicted by extrapolating the branching regression.

There is a close relationship between the branching pattern of deciduous, simple-leaved angiospermous trees and their position in the successional sequence of the deciduous forest of eastern North America (Whitney 1976). Four shade-intolerant, early-successional species had higher values of R_b (5·9

standard error 0·95) than three intermediate (4·9±0·85), and three late-successional and very shade-tolerant species (3·9±0·25). Whitney (1976) discussed these differences in relation to the proposal (Horn 1971) that, in early-successional species, the leaves are randomly distributed throughout the crown, while, in late-successional, shade-tolerant species, the leaves are held in non-overlapping monolayers. *Populus tremuloides*, and early-successional species with a large R_b (8·6), has a multiranked branching pattern with a large number of short shoots positioned around large erect branches. By contrast *Fagus grandiflora*, with a low R_b (3·5), has highly forked (tending to bifurcating) branches flattened in the horizontal plane.

The environment in which a tree grows may influence its R_b value; fast-growing trees on good sites may produce more branches, and have larger R_b values, than slow-growing trees on poor sites (Borchert & Slade 1981). However, R_b does provide a useful interpretative statistic in some situations. *Acer saccharinum* was classified by Whitney (1976) as a late-successional species with a relatively low R_b (4·4), but Steingraeber *et al.* (1979) found that open-grown trees had $R_b = 3·2$ whereas understorey trees had $R_b = 7·1$ (significantly different, $P<0·01$). Pickett and Kempf (1980) found that *Acer rubrum*, *Cornus florida* and *Viburnum prunifolium* had significantly larger values of R_b when growing in open fields as opposed to closed forest canopies ($P<0·001$). However, this difference may not exist for all species. Oohata and Shidei (1971) found that R_b was the same on experimentally unshaded and shaded seedlings of *Quercus phillyraeoides*, and Whitney (1976) concluded that open- and shade-grown *Fraxinus americana* had similar R_b values, although Pickett and Kempf (1980) noted that this species was usually under severe stress in closed forests.

Branching structures can vary within tree crowns. In *Betula populifolia*, R_b was 5·1 in the upper part of the crown and 4·2 in the lower part (Whitney 1976). In *Quercus rubra*, while R_b did not differ significantly between 16 m and the top of a 27 m tall tree, the length of both the first-order branches and the petioles was less at 27 m, and the angles which first-order branches made at nodes were more acute (44° compared with 77°).

D. Crown dimensions and timber yield

Trees growing in stands differ in crown shape, depending on the species and the trees' position within the canopy (Fig. 6A,B). The crowns of coniferous trees (excurrent form, large R_b) are greatest in diameter about two-thirds from the top ($l_d/l = 0·67$, Fig. 6C), whereas the crowns of broadleaved species (decurrent form, small R_b) are broadest nearer the tree top ($l_d/l > 0·5$, Fig. 6D).

Trees within fully stocked stands differ, in both their absolute rates of timber production (m^3 $tree^{-1}$), and in their production per unit crown projection area, crown volume and crown surface area. Assmann (1970) summarized analyses for stands of *Pinus sylvestris* and *Quercus petraea*. In all stands, large trees had the largest absolute rates of timber production both between and within three 'social classes' – dominant, codominant and dominated. However, *within* each social class, the smaller trees, which had more

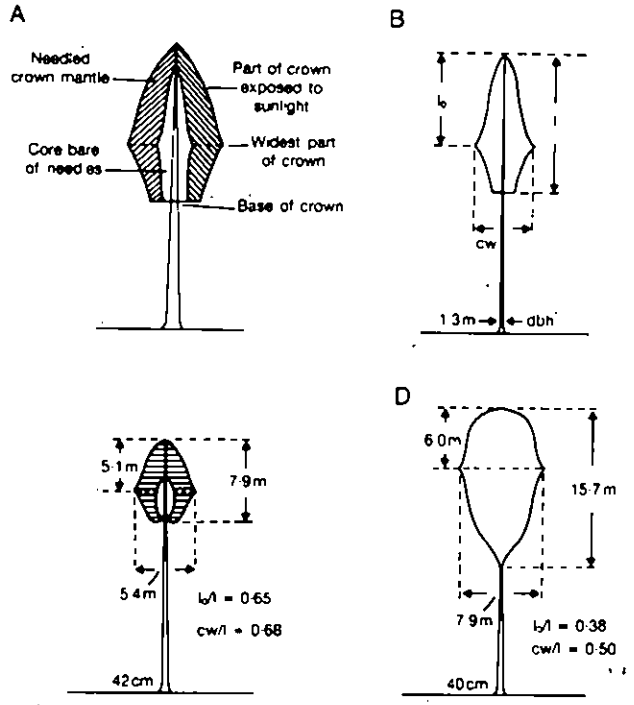

FIGURE 6. Crown dimensions of forest-grown trees showing typical differences between coniferous and deciduous species.
A. Idealized crown structure of a conifer.
B. Crown dimensions.
C. The structure of an 88-year-old *Pinus sylvestris* tree with a crown volume of 87·3 m³.
D. In contrast to C, the crown volume of an 88-year-old dominant *Fagus sylvatica* tree of similar height (25-30 m) is 356 m³, with the major part of that volume below the widest part of the crown. Note that, despite its smaller crown, the stem diameter of the *Pinus sylvestris* is greater than that of the *Fagus sylvatica*. A hypothesis to explain this difference is described in the text. (Redrawn from Assmann 1970.)

slender crowns and therefore a relatively larger crown surface area per unit of growing space, had generally greater timber production 'efficiencies', in terms of timber produced per unit ground area, crown surface area or crown volume.

With increasing crown width and crown fullness ratio (CW and CW/l, Fig. 6), the relationship between crown surface area and crown volume must change. As a crown grows, an increasing proportion of its volume is occupied by a core of supporting branches which carry no needles. This supporting structure contributes very little photosynthate, but it uses photosynthate both for wood production and respiration. Each branch must continue to thicken along its length in order to support the weight of foliage produced at an increasing distance from the trunk (see below). This demand for photosynthate by the supporting branches may explain the lower efficiency of stemwood production of the larger trees in each social class.

Surface area is the crown parameter which correlates most closely with stemwood volume increment, both in single species (Hamilton 1969), and multistorey mixed species stands (Magin 1959).

III. CONTRIBUTION OF DIFFERENT BRANCHES ON A TREE TO STEM GROWTH

The vertical distribution of trunk thickening, within and below the crowns of stand-grown trees, has been estimated in anatomical studies (Denne 1979) and by pruning living branches (Labyak & Schumaker 1954). Branches contributing most to trunk thickening are at the point of crown interaction and competition for light, and are generally above the position where branches have maximum foliage weight.

The contribution by branches to stemwood increment depends both upon their position in the canopy and their seasonal pattern of export. A comprehensive analysis of this potential has been made in *Populus* in relation to its use in short rotation coppice in the Lake States of the USA (Isebrands 1982). Leaves show a distinct hierarchy, in both photosynthetic performance, and in the destination of exported photosynthate. In two-year-old plants grown from cuttings, leaves on the current year's terminal shoots had a high photosynthetic rate over the whole season, whereas leaves on lateral branches had lower photosynthetic rates which declined in late summer. Two types of lateral shoots were produced: 'short shoots', comprised solely of leaves preformed in the bud, and 'long shoots', which also formed leaves during the current season. Within the mid-crown, shade leaves of long shoots had a higher photosynthetic potential than those of short shoots, mainly because their average leaf age was less – there being a general decline in photosynthetic potential with increasing leaf age during the season (Nelson & Michael 1982).

Very little of the photosynthate produced by leaves on lateral branches of *Populus* was exported to the leader or to other laterals (Isebrands 1982). Prior to bud-set, export was primarily to the main stem internodes below the branch and to the supporting branch itself.

Following bud-set, an increasing proportion went to the roots. Main stem height growth was achieved using photosynthate from the main stem leaves, although after bud-set they too contributed an increasing amount to roots. Differences in the timing of bud-set among lateral branches influenced the pattern of export of photosynthate: in the lower canopy bud-set could be three weeks later than in the upper canopy. However, differences in photosynthetic rate resulted in a larger total contribution to stem growth from upper canopy branches.

IV. SOME MODELS OF BRANCH STRUCTURE AND FUNCTION

The measurements of timber production per unit crown size, reported by Assmann (1970), suggest that *stand* production might be increased, if trees

were grown which maximized the ratio of photosynthesizing mantle to non-photosynthesizing cones of supporting branches within the crown. This hypothesis needs to be explored with regard to genetic improvement and stand management. What inherent attributes of branch growth are required to produce efficient crowns? And can improvements in crown 'efficiency' be maintained by management throughout the growth of the stand?

In this section, some models of branch growth are considered, which, to varying degrees, all use the concept of 'optimization of biological structure'. This concept has some disadvantages, which are discussed below, but it also yields useful insights into the relationship between structure and function.

A. R_b and the interception of light

Horton (1945) introduced the concept of R_b to describe the branching networks of rivers. The R_b of river networks in a wide variety of climates and physiographic settings is about 3·5, varying within narrow limits. Also, the length ratio between successive orders of tributaries is fairly constant at about 2·3 (Leopold 1971). As a river grows by the joining of tributaries, its course adjusts to accommodate the increased flow, and Leopold described the steady state of a river branching system as the result of a balance between opposing tendencies for (a) minimum power expenditure in the whole system, and (b) an equal distribution of power throughout the system. By analogy, he suggested that the branching patterns of trees are a balance between minimizing energy expenditure in the production of branches, and maximizing a photosynthetic surface to provide the most efficient interception of sunlight.

Leopold (1971) produced evidence for this theory in a photographic analysis of a sunflower plant. By taking photographs from different sun angles, he found that 51% of the leaf area was exposed to sunlight over a day, compared with 46% of a hemisphere with the same total surface area. The sunflower plant had 21 leaves, supported by 3·8 m of petioles and stems, whereas the length of a second-order branching system needed to support the hemisphere, divided into 21 units, was five metres. Compared with the hemisphere, the sunflower had a greater surface illumination and less branch support, so that the ratios of sunlit hours to stem lengths were 4·5 and 2·8 for the sunflower and hemisphere, respectively.

Tree branching systems do not follow a single branching rule, as river systems appear to do. Neither do they minimize path lengths (stems) to reach a network of points (leaves), in the way in which the bronchial tubes ($R_b = 2·8$), and bronchioles ($R_b = 2·3$) do to reach the alveoli in lungs (which Barker *et al.* 1973 speculated optimizes bidirectional gas flow). Leopold (1971) proposed that small and large values of R_b represented two different ecologically based strategies, in terms of yield.output per unit of energy input. In shaded situations, self-shading is avoided by producing the minimum branch length to ensure a regular, non-overlapping leaf distribution; R_b is then small and there is a continuous outward development from many growing points. In more open situations, as occur early in a succession, when typically there is all-round illumination and a requirement for rapid height growth, R_b is large,

and there is minimal expenditure on a branch support system between the main stem and the foliage.

Conifer needles have lower maximum photosynthetic rates per unit area or weight than deciduous broadleaves (Ford 1984), but conifer needles are retained for more than one year, and Schulze *et al.* (1977a) found that 47% of the CO_2 uptake in crowns of *Picea abies* occurred in needles three to four years old. Thus, for evergreen conifers, there is a premium on producing a branching structure which enables light to penetrate to the older needles, and this is just what a high value of R_b does, at least around the periphery of the crown. This fact also has an important consequence for the shade crown. From the results of simulating the light climate of *Pinus sylvestris* crowns, Oker-Blom and Kellomäki (1983) suggested that, in most situations, within-plant shading was considerably greater than between-plant shading, and that the light conditions of an individual tree were, to a high degree, determined by its own structure, and particularly by the very clumped nature of foliage. This structure is also a consequence of a high R_b. Schulze *et al.* (1977a) estimated that, in *P. abies*, 71% of the annual CO_2 uptake occurred in the sun crown. Also, branches in the shade crown of *P. abies* contributed considerably less (29%) to seasonal CO_2 uptake than those of *Fagus sylvatica* (48%).

The development of a branching structure with a low R_b value, and its relationship to light interception, was studied by Fisher and Honda (1979a), who simulated the branch generating process of *Terminalia catappa*. This tropical species has regularly bifurcating branches, produced in pseudo-whorls along the main stem, which become dorsiventrally flattened with age. Each branch produces a cluster of leaves at its distal end, and one of the new branches of the bifurcation predominates. In successive growth periods, leaves are produced at the distal end of each branch segment so that the leaf positions remain unchanged.

Fisher and Honda (1979b) calculated the total simulated leaf area of each branch, and its horizontal projected area, as branching angles and other structural features were varied. They attempted to determine the structure which maximized the average effective unshaded (non-overlapped) leaf area per leaf cluster, or that which minimized the leaf area produced by a branch or tier of branches to ensure full light interception.

The measured branching angles for *Terminalia catappa* were $\theta_1 = 24{\cdot}4°$ SE$\pm 0{\cdot}7°$ and $\theta_2 = 36{\cdot}9°$ SE$\pm 0{\cdot}0°$ for the minor axis. (That is, when a branch bifurcated, one went 24·4° to the left, the other 36·9° to the right.) The conditions in the simulation model which most closely reproduced these angles were second-order branching and either uniform or mixed symmetry in the tier of branches, ie the first θ_1 was in the same or in mixed directions for successive branches around the pseudo-whorl. Optimum branching angles varied, as both the number of branches in a tier, and the order of branching were increased. Branching angles which produced optimum light interception became increasingly asymmetric (ie the difference between θ_1 and θ_2 increased) as branch order was increased, a situation *not* found in real trees. Thus, it is possible to design trees which are more efficient in light interception than those which exist! Of course, other aspects of the growth process must

be considered. Fisher and Honda (1979a) found that the ratio of branch lengths between the two arms of the bifurcations was considerably lower for measured trees than those giving optimum light interception simulations. They suggested that branch length ratios were more closely related to considerations of branch strength than to light interception. Whilst Fisher and Honda (1979a,b) demonstrated the effectiveness of a bifurcating branching system in intercepting light, they also revealed constraints which may have limited the evolution of an optimal structure.

B. Wood increment and branch support

The role which branch length may play in foliage display must be considered in relation to the weight of the branch itself. A branch deflects under its own weight (Fig. 7A), and the deflection of the tip, Δ, relative to the branch length, depends upon the taper of the branch (McMahon & Kronauer 1976). If we assume that a branch decreases in diameter – moving outwards from the trunk – the imaginary point where the diameter is zero is the virtual origin,

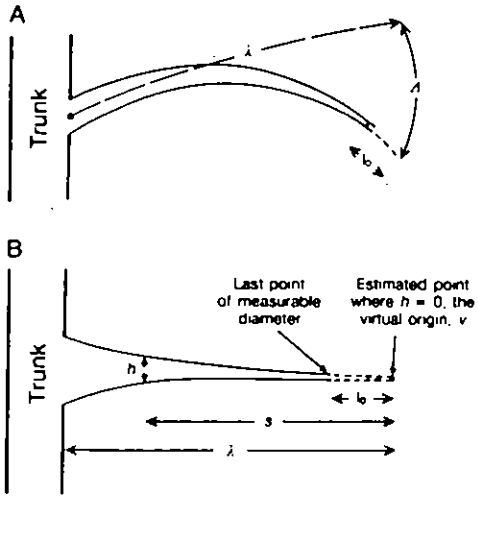

FIGURE 7. Control of branch deflection by the vertical diameter of the branch. $h = ks^{\beta}$, where k is a constant; when $\beta = 1{\cdot}5$, branch deflection under its own weight maintains a constant ratio Δ/λ (see text).

v (Fig. 7B). Then, the taper of the branch in both its vertical dimension, h, and its horizontal dimension, b, (where $h = b$ if the branch is circular) can be expressed by the power laws:

$$h = k_1 s^{\beta} \text{ and } b = k_2 s^{\alpha} \tag{4}$$

where s is the distance from the virtual origin, v, to the point where the diameter is being considered, and k_1 and k_2 are constants of proportionality. If β (the rate of taper) is 1·5, the branch is elastically self-similar; that is, the deflection of the tip, Δ, divided by its overall length, λ, is a constant, however much λ may vary, and whatever the value of α (Fig. 7B). Note that the deflection depends only upon the rate of taper in the vertical direction, so that a branch in plan view (Fig. 7C) has the same properties of deflection as square or round section cantilevers. For engineering purposes, beams may be designed with different tapers to meet different purposes; for instance, if $\beta = 2$, the beam has uniform stress along both its upper and lower surfaces.

To estimate the relationship between h and s in tree branching systems, McMahon and Kronauer (1976) first had to determine an 'average path length', L_t, from the point where h was measured (distance l_0 from the virtual origin, v) to m end twigs, where:

$$L_t = (s - l_0) = L_t = \frac{1}{m} \sum_{i=1}^{m} l_{ij} \tag{5}$$

A curvilinear relationship is obtained between L and h, with L decreasing more rapidly than h at small sizes. This is because the real measurement of diameter can necessarily only begin at the tip of a twig, and not at the virtual origin. To estimate λ_0 – the distance from the furthest real measurement to the virtual origin – McMahon and Kronauer (1976) used an iterative least squares technique. For the mean of five deciduous trees, they found $\beta = 1{\cdot}50$ with maximum 1·66 and minimum 1·37. To augment these estimates of β, McMahon and Kronauer (1976) used an interesting property of beams – their natural frequency when freely vibrated is related to β. In particular, for $\beta = 1{\cdot}50$, the natural frequency of vibration is proportional to λ^{ψ} with $\psi = -0{\cdot}50$. McMahon and Kronauer measured the natural frequency of branches of different lengths, and of whole trees, both with and without leaves, and found an average exponent, $\psi = -0{\cdot}59$. They concluded that the taper of vertical branch diameter approximated to the model of 'elastic similarity'. Because vertical branch diameter controls the mechanical properties of branches, trees may have very different R_b values, yet have the same *mechanical* design. They proposed that maintaining a constancy in branch taper ensured that tree crowns maintained their regular form as the tree grew.

C. Interactions between R_b, branch strength, branch growth and stemwood increment

Whilst, in engineering terms, the bending properties of branches and trunks may be independent of R_b, the requirement that branches should increment a specific amount of wood to maintain a certain taper obviously places a specific demand for photosynthate upon the foliage. The pattern of photosynthate movement in *Populus* described above indicates that, after the first year of

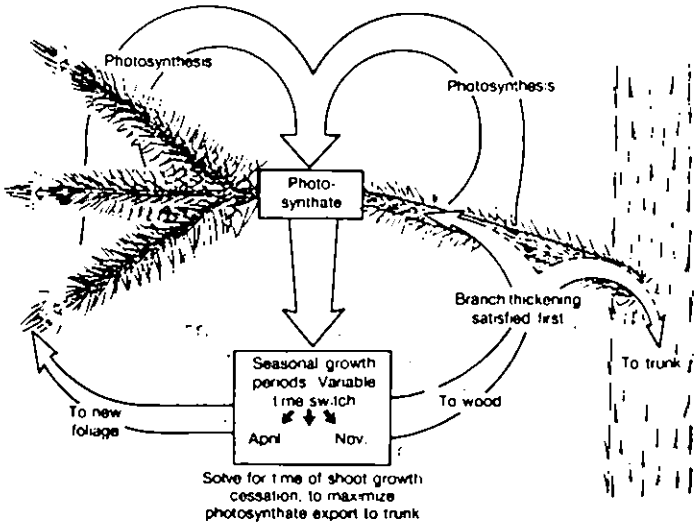

FIGURE 8. Diagrammatic representation of a model, describing the effect of varying the annual investment in new foliated shoots on branch thickening and photosynthate export to the trunk.

growth, branches do not import photosynthate. If we assume this hypothesis to be generally true, then the investment in new foliage, the requirement for branch thickening, and the export of material to the stem together constitute a dynamic system (Fig. 8). This system was simulated for a conifer branch growing in its second year, where the branching frequency, R_b, the rate of taper in branch diameter, β, and the exponential rate of decline in photosynthetic rate per unit needle weight with age were all varied (Fig. 9). An eight-month growing period was assumed, and the simulation calculated the amount of new foliated branch produced to optimize export to the stem. The optimal branch length was sought, by allowing the 'duration' of shoot extension to vary, during which time all of the photosynthate from the old foliage and 50% of that from the new foliage went to produce new branch length and associated needle weight. New branches were all 'grown' from the distal end of the previous year's branch. During the period after shoot elongation was completed, photosynthate was first allocated to branch thickening – to the diameter required by β using measured constants – and the remaining photosynthate was exported to the trunk. Whilst investment in new branch increased the total photosynthate produced, the additional length obviously placed a greater demand on photosynthate for branch thickening.

As R_b was increased in the simulations, so the material returned to the stem increased, as also did the total length of new shoot produced. That is, it cost less, in terms of branch thickening, to produce new shoot length on many rather than few branches. This is a crucial feature of branch design.. The duration of shoot growth which maximized export to the trunk also increased with increase in R_b (ie finely divided branches should grow for longer), because there was less requirement for branch thickening material (Fig. 9). Decreasing β increased the material exported to the trunk.

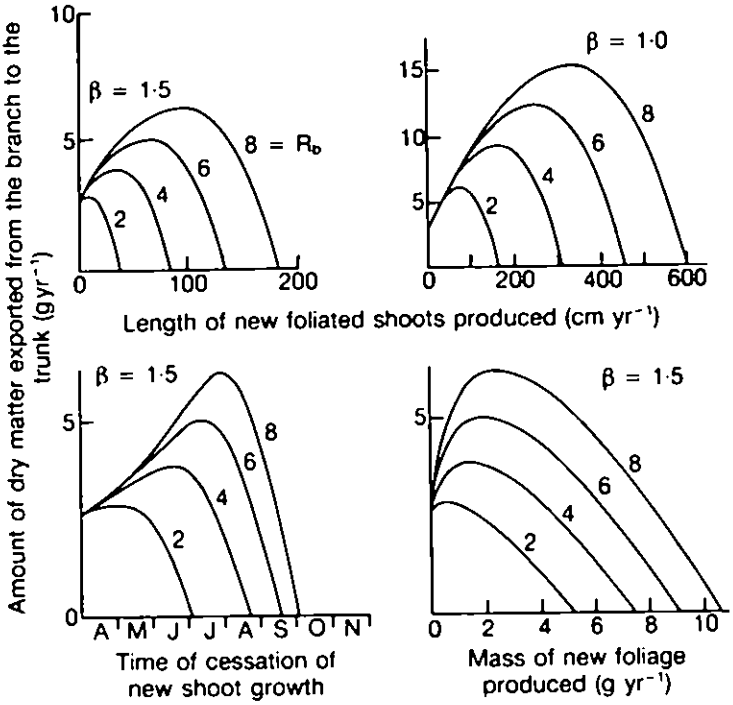

FIGURE 9. Results of simulations of the effect of varying the bifurcation ratio, R_b, (over the range 2 to 8) and the coefficient of branch diameter thickening, β, on branch growth and the export of photosynthate to the trunk. Values used were those measured on *Picea sitchensis* (Ford 1982a, and unpublished data): initial branch length was 25 cm with 0·05 g needles cm^{-1}, wood density 0·5 g cm^{-3}, photosynthetic rate $Pn = 3{\cdot}5^* 0{\cdot}7^{t-1}$, branch diameter at 5 cm from the tip, $d = 0{\cdot}004v^{\beta}$ where v was the 'virtual origin' (see text and Fig. 7).

D. Are branches optimum structures for stemwood production?

Models of the type described above could be used to develop specifications for the branching structure of an ideotype. However, the use of optimization criteria requires great care.

It may not be valid to assume that branching structures maximize photosynthetic gain per unit investment in branch material. Natural selection operates through breeding success, and features other than simply the growth rate of the plant can influence this factor. Fisher and Honda (1979b) drew attention to Ashton's suggestion that the adaptive value of the pagoda habit in young plants is the ability rapidly to expose new leaf surface in dense layers above competitors (Ashton 1978). Equally, it may not be valid to assume that branching structures develop to optimize light interception, because factors other than light may limit growth. Paltridge (1973) modelled tree growth and structure as a balance between light interception and water stress, which he

considered would be likely to increase as trees become taller. This balance was also the underlying rationale of Brunig's (1976) classification.

When modelling branch growth, the criteria should include the selective pressures under which the tree has evolved, and the environmental conditions under which it currently functions. Selective pressures determine the genotype, and so set the rules which branching follows. However, as with any character, there is heterogeneity within populations, and in the broad ecological context there may not be an optimum structure for individuals within a species. Continued breeding success requires sufficient variation between individuals to survive under the differing conditions typical of the species habitat.

There is also evidence that the control of branching is not completely rigorous. Cochrane and Ford (1978) fitted statistical distributions to rules governing branch production, extension and dispersion in *Picea sitchensis*. These rules were used in a simulation model of crown growth (Cochrane 1977). An important feature was that simulated trees were visually 'unreal', both when the variance was reduced to zero or was doubled. A similar result was found in the simulation of rooting patterns (Henderson *et al.* 1983). These findings have important implications for our understanding of biological branching systems, and for our attempts to fit models to data. Biologically, the existence of a significant variance term implies a 'slackness' in the control system under study. Generally, Cochrane (1977) found that the variance for relationships within the canopy increased for the slower, less productive branches.

V. CHANGES IN BRANCHING AND FOLIAGE AMOUNT DURING PLANTATION DEVELOPMENT

The production and growth of branches change as the canopy of a forest plantation passes through different stages of development. These changes may have an important impact on both total timber production and its distribution between individual trees. A crop of *Picea sitchensis* provides an example.

A bud of *P. sitchensis* extends in one year, and in the next year acts as a source of whorl and interwhorl branches (Cochrane & Ford 1978). Each bud may produce a similar sequence of branches, but, as they become submerged in the canopy, branches gradually fail to produce first their own interwhorl, and then whorl branches, and finally they fail to elongate at all (Longman, this volume). Cochrane and Ford (1978) found that, during canopy development, separate rules governed the production, dispersion and extension of branches along the main stem of the tree. However, branch dispersion followed consistent rules from year to year. For instance, whorl branches were always arranged in a spatially regular (not random) fashion around the stem, irrespective of their numbers; interwhorl branches were absent immediately below their distal whorl and above their proximal whorl; and the angles between the vertical main stem and the branches increased from the top of the tree towards the base of the crown, especially for interwhorl branches.

Cochrane and Ford (1978) advanced the hypothesis that there was within-

tree competition for resources during the early years of growth, which was related to the numbers of branches produced by a tree on its main stem. There was a marked decrease in the number of whorl branches produced each year after the branches of neighbouring trees met ('foliage overlap', Fig. 10), which was related to an increase in leader growth rates. Prior to year six, leader growth accelerated by some $5{\cdot}2\,cm\,yr^{-1}$. Between years seven and ten, the increase in leader increment was $8{\cdot}2\,cm\ yr^{-1}$, and over this period annual leader extension was negatively correlated with numbers of whorl branches produced per year. While the leaders certainly exerted apical control over the whorl branches, the whorl branches also influenced leader growth. Individual trees were affected to different extents by this process, because individuals differed significantly in the numbers of whorl, and particularly interwhorl, branches they produced.

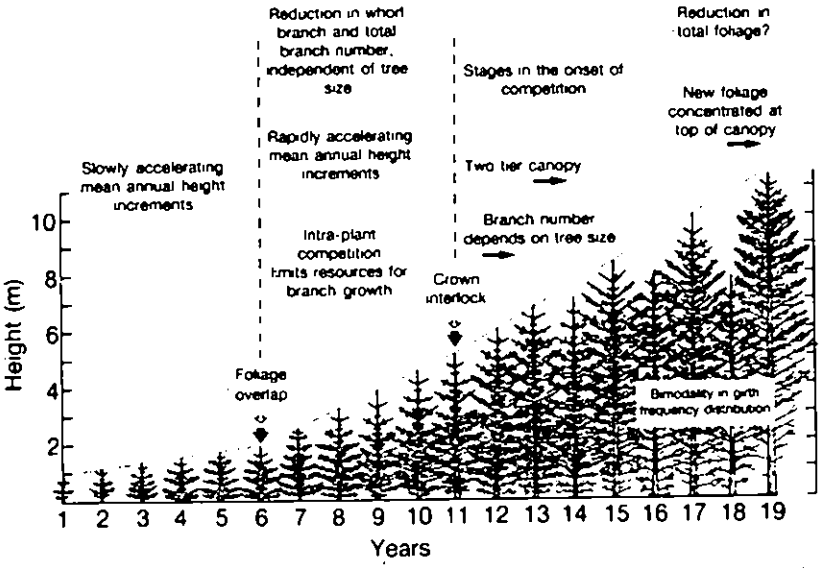

FIGURE 10. Controlling influences on branch growth and canopy function in a developing plantation of *Picea sitchensis* in Scotland.

From year 11 onwards, mean annual height increment stabilized. Large trees produced most branches, and had greatest leader growth, and Cochrane and Ford (1978) suggested that this stage in canopy development ('crown interlock', Fig. 10) marked the onset of between-tree competition. However, whilst this was apparent in the numbers of branches produced at the top of the canopy, competition in terms of trunk diameter increment appeared only at year 16 (Ford 1982a). This delay may reflect the length of time taken for changes in the top whorls of the tree to have an effect on wood production in the trunk.

At year 16, new shoot production shifted from being evenly distributed throughout the crowns to being concentrated at the tops. The canopy changes quite quickly, from being akin to a collection of long but bush-like crowns,

to a two-tier mixture of a few dominant trees and many dominated trees. Associated with this change, there was a decrease in leaf area index of 11% between years 16 and 18 (Ford 1982b). Similar decreases have been found in plantations of other coniferous species at the same stage of development – for instance, 24% during two years after attaining a maximum at age seven in *Pinus radiata* (Forest & Ovington 1970) and 23% during the 20 years following a maximum at age 11 in *Cryptomeria japonica* (Kira & Shidei 1967). Isebrands and Nelson (1982) discussed the same effect in short-rotation *Populus*, which they suggested signalled a decline in productivity owing to crown competition.

I suggest that total foliage amount decreases because dominant trees shade smaller neighbours by producing lateral branches, while the centres of their own crowns become increasingly bare. The foliage 'lost' from the canopy, owing to the 'decline' of suppressed trees, is not made up by additional foliage increment on the large trees. Assmann (1970) reported a suggestion made by Metzger in 1893 that the maximum volume increment per unit land area in even-aged coniferous forest stands is reached early in the life of the crop, before the insolated parts of the crowns have developed a bare inner core.

VI. GENETIC VARIATION IN STEMWOOD PRODUCTIVITY AND BRANCHING IN OPEN-GROWN CONIFERS

In young, widely spaced trees, large within-species genetic differences have been found in the production of stemwood relative to branchwood. Matthews *et al.* (1975) estimated that stemwood production on *Pinus virginiana* could be increased by 30%, if family differences in total wood production could be combined with differences in stem/branchwood proportion. They examined open-pollinated progenies, from 20 *Pinus virginiana* parent trees, selected equally from naturally well and poorly pruned trees. At the onset of crown closure (age eight), when branch weights were a large proportion of total wood weights, families differed significantly in stem/branchwood proportion from 0·48 to 0·61 (see Cannell, this volume).

Tallness, sparse branching, and the absence of large basal branches were the most important characters positively correlated with large and efficient stemwood production (per unit of foliage mass or area) in clones of *Pinus contorta* and *Picea sitchensis* (Cannell *et al.* 1983). Seven clones of both species were grown at a lowland 'agricultural' site, and at age eight (before crown closure) the species had similar stem dry weights (2·76 and 2·87 kg tree^{-1}, respectively). However, there were differences between species in branch and foliage structure. *P. sitchensis* had only 56% as much branch weight, and 61% as much foliage weight, as *Pinus contorta*. Within both species, there were significant differences between clones in stem/branchwood proportion and in stemwood production per unit foliage mass and area. The latter (stemwood production per unit of foliage) was *negatively* correlated with percentage needle weight on the tree (ie poorly foliated, sparsely branched trees were relatively 'efficient').

The potential for exploiting these differences depends on how stable they

are as the environment changes during stand development. Differences among clones of *P. sitchensis* in stemwood amount may reflect differences in both the overall efficiency of wood production and in the allocation to different tree parts. Four of the *P. sitchensis* clones were also grown at a high-altitude site in a poor soil. At this site, total dry matter production, and foliage amounts were less by different amounts for the four clones than at the lowland site, but for each clone the production of total wood (branches plus stem) per unit of foliage was the same as at the lowland site.

VII. CAN WE INCREASE PLANTATION YIELD BY GENETIC MANIPULATION OF BRANCH CHARACTERISTICS?

In the study of Cannell *et al.* (1983), the principal morphological characteristic associated with large stemwood production per unit of foliage was sparseness of branching. This characteristic is also considered to be desirable in the ideotypes formulated by Dickmann and by Kärki and Tigerstedt (this volume). If such genotypes were grown in stands, would they give an increase in productivity per hectare?

Crown shape, particularly the ratio of crown surface area to crown volume, greatly influences stand productivity. If this ratio were kept high for longer into the rotation, branch thickening would presumably require less photosynthate and, because the phase of intense crown competition would be postponed, a large foliage area might be maintained for longer. However, to achieve these effects, the trees would have to be close enough to occupy the site. A precise silviculture would have to be worked out. There may be an interesting parallel in the potential for increasing grass yields (Rhodes 1971) or grain yields in maize (Pendleton *et al.* 1968) by growing more erect-leaved genotypes – substantial gains can be achieved, provided that a large enough total canopy is maintained to give high light interception.

I suggest that the possibility of increasing stemwood yields by minimizing branchwood increment will vary between trees of different branching habit and broadly, but not exclusively, between conifers and broadleaved deciduous trees. The essential attribute of the more productive conifer genotypes discussed in the previous section is that they produce less branchwood, so the foliage they grow is closer to the stem. This decreases the requirement for branch thickening, and may reduce self-shading in the crowns. In stands, the canopy would be composed of long columnar crowns, and the strategy should be to increase the longevity of needles and to increase the 'return on investment' in foliage. Illumination levels lower down the tree would increase, but of course other factors, notably nutrition, may also influence needle longevity and canopy structure (Brix 1981).

Late successional broadleaved trees have low values of R_b. This may ensure a spatially more even distribution of foliage throughout the shaded portion of the canopies, but probably implies greater investment in branch thickening per unit length of branch. The growth strategy of these broadleaved trees is different from that of conifers, and probably the strategy for tree improvement should differ also.

In field trials of clonal *Triplochiton scleroxylon*, Leakey and Ladipo (1985) found that, at wide 4·9 m spacings, the trees with fewest branches per unit length of stem were tallest and had greatest stem diameter after 18 months. However, after canopy closure and some branch abscission, there was an even stronger positive relationship between stem diameter and the total number of branches remaining on the trees. Leakey and Ladipo (1985) suggested that, after canopy closure, the ability of branches to survive shading, and not self-prune, became an important determinant of stemwood yield. So, whilst an effective strategy to increase the productivity in conifers might be to concentrate on increasing crown surface area, it might be insufficient in those hardwoods which achieve a substantial proportion of their stemwood increment from branches in the shaded part of the crown.

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